Marine Environmental Research **12** (1984) 113–126

Abrasive Effects of Mount Saint Helens Ash Upon Epidermis of Yolk Sac Larvae of Pacific Herring *Clupea harengus pallasi*

George W. Boehlert*

College of Oceanography and Marine Science Center,
Oregon State University, Newport, Oregon 97365, USA

(Received: 14 November, 1983)

ABSTRACT

Larval Pacific herring Clupea harengus pallasi *were exposed for 24 h to suspensions of estuarine sediment and volcanic ash from 0 to 8000 mg/litre. The effects of these suspensions on the epidermis of the yolk sac larvae were determined using light and scanning electron microscopy. Examination of the epidermis at specific locations on dorsal and ventral body surfaces showed that the effects were apparent with increasing concentrations of both sediment and ash. The effects of volcanic ash, however, occurred at lower concentrations and were of greater magnitude than those of sediment. Examination of the epidermis of these larvae under the scanning electron microscope revealed puncture-type damage associated with volcanic ash but not estuarine sediment. Thus, in addition to the possible effects of smothering which may occur with fine particulates, the ash particles result in direct mechanical damage to the delicate early larvae. The concentrations where effects were noted were greater than those likely to be observed in the lower Columbia River estuary where the larval herring occur. In upriver locations characterized by higher suspended particulates, delicate larvae of other species may suffer epidermal damage.*

* Present address: Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, PO Box 3830, Honolulu, Hawaii 96812, USA.

Marine Environ. Res. 0141-1136/84/$03·00

INTRODUCTION

The eruption of Mount Saint Helens had far-reaching effects on aquatic resources from the headwaters of the Toutle River to the Columbia River estuary, and was even noted offshore in the Columbia River plume waters (Baker & Curl, 1981). Virtually all of the fish in the Toutle River, and the Cowlitz River below its confluence with the Toutle, were killed (Martin *et al.*, 1982). Shoals of ash and mud up to 7·6 m deep were found in the Columbia River; these deposits have also been carried to the estuary where shoaling has been noted near the port of Astoria. Some 10·7 million cubic yards of sediment would have to be dredged to return the river to its original dimensions. Dredging may increase particulate loads in downstream locations and impact fishes. Resultant sedimentation and higher suspended particulate loads may alter the fishes' physiology (Redding & Schreck, 1982), behavior (Gardner, 1981; Swensen & Matson, 1976), and have other effects (Muncy *et al.*, 1979). These effects may affect fishes of the lower Columbia River estuary, a nursery area for many marine fish species (Misitano, 1977); increased sedimentation rates may affect reproduction, hatching and larval survival, as has been noted in other habitats (see Muncy *et al.*, 1979 for a review). Ash particles may have further detrimental effects on epidermal and gill tissues of fishes; more devastating effects might occur in delicate tissues of early larvae, which are more susceptible to sublethal effects than are later life stages.

The effects of suspended ash upon fish larvae have not been studied; research studies on salmonids began almost immediately after the eruption, but the results are not completely clear. The Toutle and Cowlitz River system had large runs of economically important salmonids before the volcanic eruption. The immediate effect on these fish was devastating, as shown by live box bioassays, but lethal effects may have resulted from stresses other than suspended particulates alone (Stober *et al.*, 1982). Other sublethal effects of volcanic ash have also been examined in salmonids. Volcanic ash is composed primarily of silica (Fruchter *et al.*, 1980), that has sharp, angular characteristics which might enhance abrasion. Although early reports detected abrasion and puncturing damage by ash particles from fish in live boxes (T. Yasutake, pers. comm.), Stober *et al.* (1982) found no effect of suspended ash on the structure of gill tissue or upon the subsequent ability of smolts to enter seawater or perform in swimming trials. Under short-term conditions, Redding & Schreck (1982) also found no mechanical abrasion of the gills.

Volcanic ash may nonetheless lower the chances of subsequent survival of fish, and its sublethal effects may become more pronounced when other stressful factors, such as increased water temperature or velocity, are evident.

We know that survival of the egg and larval stages of marine fishes is important to population dynamics; it has been suggested that critical periods of heightened mortality at these stages may result in the determination of year class strength (Hjort, 1914; Hunter, 1976). While some factors may be severe enough to cause larval mortalities, sublethal stresses have important effects upon fish eggs and larvae (Rosenthal & Alderdice, 1976).

The overall goals of this research are to determine the abrasive effects of suspended ash and estuarine sediment on the epidermis of larval Pacific herring, *Clupea harengus pallasi*—a marine species which spawns in the lower Columbia River estuary. This species has adhesive, demersal eggs, a common characteristic among estuarine-spawning fishes. It is an important resource in the northern Pacific, both as a commercial catch and as forage for other important species.

MATERIALS AND METHODS

The preparation of volcanic ash and estuarine sediment for these experiments is described in Boehlert & Morgan (in preparation). Particles larger than 24 μm were removed by settling over a 10 cm water column. This resulted in a particle size distribution smaller than that used in other experimental studies (Stober *et al.*, 1982; Redding & Schreck, 1982), but was necessary in order to maintain suspensions for the work on fish larvae. Final particle sizes of volcanic ash and estuarine sediment were analyzed with a Coulter®* counter and were slightly different, with 96 % (by weight) of both ash and sediment between 3 and 19 μm.

Experiments were designed to evaluate the effects of suspended sediment and ash on the epidermis of newly hatched herring larvae. The experiments were carried out on 19–20 March, 1982 with eggs which had been spawned naturally on the north jetty of Yaquina Bay. All eggs and larvae were maintained in seawater adjusted to 15‰ salinity at 10 °C. After hatching, groups of 20 larvae were placed in individual 1-litre

* Coulter® is a registered trade name of Coulter Electronics Inc., Hialeah, USA.

containers held within 10-litre tanks. The 1-litre containers had a 335 μm nylon mesh bottom to allow free flow of sediment and ash suspensions. Larvae were introduced into duplicate containers at six levels of suspended ash or sediment (0, 500, 1000, 2000, 4000 and 8000 mg/litre). Each 2 h the suspension was replaced with a new 1-litre volume slowly siphoned into the vessel. Over the 2-h interval, the ash and sediment concentrations decreased through settling to approximately 25 % of the initial values. After 24 h, the larvae were removed to petri dishes and enumerated as either dead or alive, based upon presence or absence of heartbeat. Live larvae were subsequently preserved for later microscopic analysis in 2 % buffered glutaraldehyde in teleost saline.

Preserved larvae were randomly selected and subsequently processed for histological analysis following the techniques of O'Connell (1976) and serially sectioned at 6 μm on a rotary microtome. Sections were mounted on glass slides and stained with Harris' hematoxylin and eosin-phloxine B. Sectioned specimens were examined under a microscope for evidence of abrasion to the epidermis in yolk sac experiments. All larvae were identified with random numbers and were examined without knowledge of the experimental treatment. Two areas were chosen for detailed histological analysis of epidermal structure. The first was the epidermis on the ventral surface of the yolk sac, the second the epidermis on the dorsal surface in the region of the nape, just posterior to the head. In serial sections from each larvae, four sections from the areas of interest were randomly chosen and examined at 1000 magnification. Each of these sections was graded on a qualitative basis from 1 (good, characteristic of normal fish) to 3 (poor, characterizing severely abraded epidermis). The criteria for these assessments are as follows:

1. Good, epidermis smooth at surface, characterized by some small protrusions. Occasional eosinophilic vesicles, particularly in the ventral region. No separation of epidermis from underlying tissues or shrinkage apparent (Fig. 1D).
2. Intermediate, epidermis smooth to slightly abraded, with thin, irregular eosinophilic processes differing from the protrusions noted above. Some separation of epidermis from underlying tissues.
3. Poor, external surface of epidermis rough, with apparent abrasion and epidermal puncturing. Frequent separation of epidermis from underlying tissues (Fig. 1, E and F).

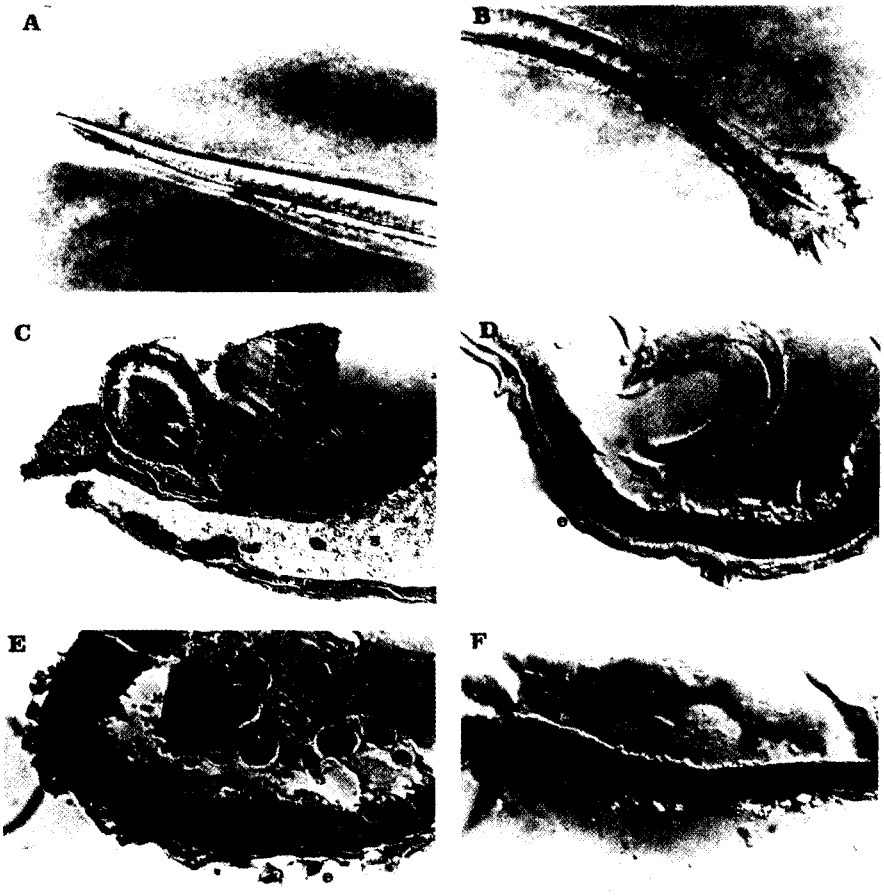

Fig. 1. Photomicrographs of the epidermis and finfold of yolk sac larval *Clupea harengus pallasi* exposed to various concentrations of ash or sediment for 24 h. A. Caudal region from a larva in the control. The finfold is generally intact with the exception of minor damage to the most posterior region. B. Caudal region from a larva exposed to 2000 mg/litre volcanic ash. Note the irregular nature of the finfold and the abrasion to the margin, particularly on the caudal finfold. C. Head region of a larva from the 1000 mg/litre sediment exposure. Note the sediment particles in the gullet; the gut in this yolk sac larva is not yet open (720 ×). D. Epidermis in the yolk sac region of a larva exposed to 2000 mg/litre sediment. The epidermis is smooth and uniform and was graded as condition 1 (cross-section, 3500 ×). E. Epidermis in the yolk sac region of a larva exposed to 4000 mg/litre sediment. The epidermis was graded as condition 3 (poor). Note the deterioration and rough surface (cross-section, 2200 ×). F. Epidermis from the yolk sac region of larva exposed to 8000 mg litre volcanic ash. The epidermis was graded as condition 3 (poor); it is discontinuous and abraded (longitudinal section, 2200 ×). e, epidermis; y, yolk mass; s, sediment particles; f, finfold; r, retina.

While examining these histological sections, care was taken to ignore damage from histological procedures, which was occasionally present as section fracturing; this was particularly apparent on the yolk sac epidermis, where the brittle yolk is difficult to section smoothly. After the four sections were examined from each specimen and the condition assigned, a mean value for each area was determined. The mean of these mean values for a number of specimens is presented as the value for a given ash or sediment concentration of suspensions. Within areas and treatments, the effects of concentration were determined with one-way analysis of variance.

Specimens were also prepared for scanning electron microscopy. Larvae were prepared for observation following the procedures of Dobbs (1974). Briefly, larvae were preserved in 2% glutaraldehyde, dehydrated through a graded series of alcohols, and put in two changes of liquid freon. Larvae were placed in small porous capsules and processed in a critical point dryer. They were mounted on studs using double stick tape and coated with a thin layer of gold–palladium in a vacuum evaporator. These specimens were examined on an AMR 1000 scanning electron microscope. Particular attention was paid to the epidermal tissues and the presence of ash- or sediment-related damage.

RESULTS

Larvae generally appeared to be in worse condition in the higher concentrations of ash. This assessment was based upon condition of finfold and probable epidermal damage observed under the dissecting microscope. While finfolds in sediment often had adhering particles, they were not abraded as in higher ash concentrations (Fig. 1, A and B).

Mean mortality rates over all concentrations, including controls, were 5·40% (SE 1·65%) for ash and 5·28% (SE 2·35%) for sediment. No differences in mortality were apparent between controls and the suspensions of ash and sediment at the end of the 24-h exposures, despite an apparent difference in the epidermal condition of larvae (Fig. 1, A and B). Larvae were not maintained beyond the 24 h period, however, to evaluate sublethal stress and possible subsequent mortality. In examination of the histological preparations, about 65% of the scores within sections agreed. Mean scores showed a general trend of increase with increasing ash or sediment concentration in both dorsal and ventral

TABLE 1
Histological Assessment of Epidermal Structure in Larval Pacific Herring[a]

Region	*Concentration* (*mg/litre*)	*Volcanic ash*			*Estuarine sediment*		
		N	$\bar{X}$	*s*	*N*	$\bar{X}$	*s*
A. Ventral yolk sac	0	10	1·35	0·36	10	1·35	0·36
	500	5	1·75	0·56	4	1·25	0·20
	1 000	5	1·90	0·52	3	1·33	0·14
	2 000	6	2·00*	0·72	3	1·42	0·29
	4 000	6	1·96*	0·56	5	1·65	0·65
	8 000	6	2·03*	0·49	4	1·63	0·32
B. Dorsal nape	0	9	1·11	0·13	9	1·11	0·13
	500	3	1·25	0·25	4	1·13	0·14
	1 000	5	1·65*	0·29	3	1·33	0·14
	2 000	3	1·83*	0·29	3	1·25	0·25
	4 000	6	1·96*	0·19	5	1·45*	0·21
	8 000	5	1·87*	0·31	3	1·75*	0·25

[a] Four sections of epidermis on each specimen were graded on a subjective scale of 1 (good) to 3 (poor) for dorsal surface and ventral yolk sac regions. Values in the Table represent the mean value in each treatment. Experiments were run concurrently and controls were combined. Asterisks indicate treatment means significantly different from the appropriate controls (ANOVA, LSD, $P < 0{\cdot}05$). *N*, number of specimens; $\bar{X}$, mean ranking; s, standard deviation.

epidermal areas (Table 1). In the controls, the mean score was better for the dorsal than the ventral (yolk sac) region. For the ventral epidermis, there were no significant effects of increasing sediment concentration on epidermal structure, whereas effects were noted due to volcanic ash exposure with significant mean scores at suspensions greater than 2000 mg/litre. In the dorsal nape region, greater effects were noted for both estuarine sediment and volcanic ash. Controls were significantly different from the sediment concentrations of 4000 and 8000 mg/litre, and from all ash concentrations of 1000 mg/litre and greater (Table 1). Since the same controls were considered for both ash and sediment, the abrasive effects of ash were greater than those of sediment.

Observations with the scanning electron microscope are in general concurrence with the histological observations. Observations of the lateral epidermis of control yolk sac larvae show structures typical of developing teleost epidermis (Roberts *et al.*, 1973), with distinct cellular borders and microridges (Fig. 2A). Small, irregular particles, possibly associated with the processing, were occasionally apparent. The margins

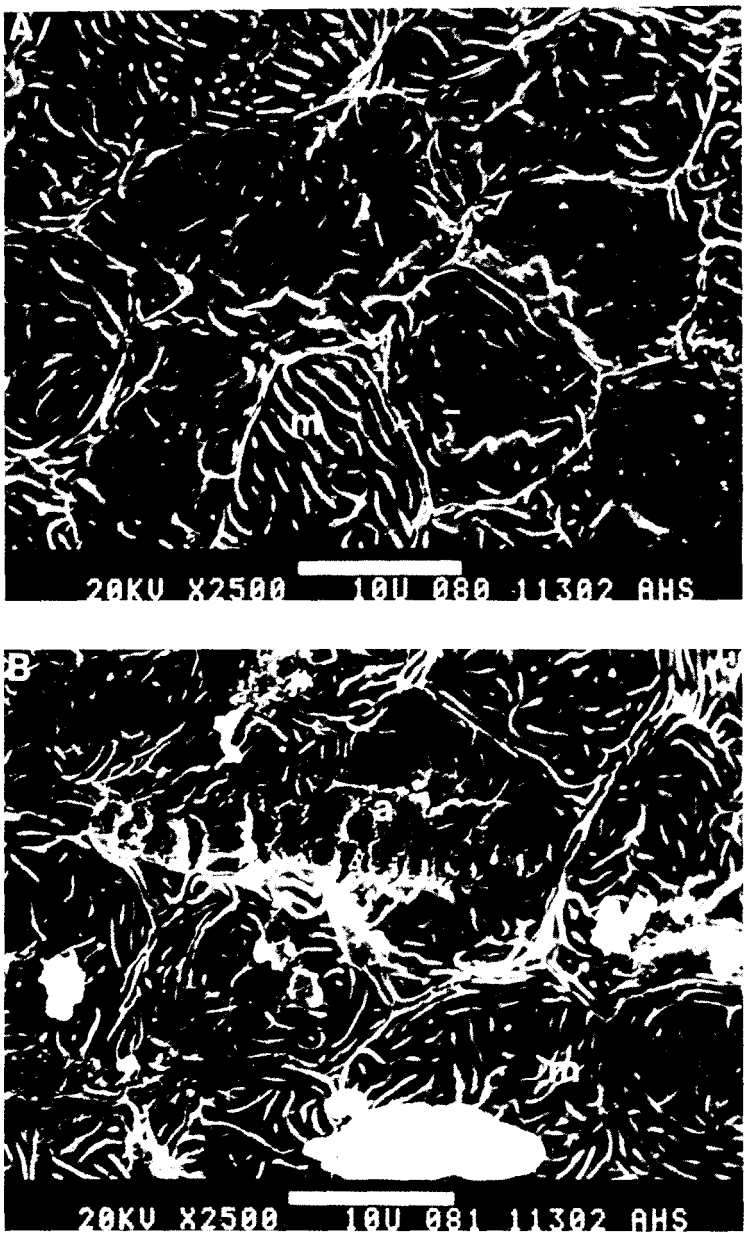

Fig. 2. Scanning electron micrographs of the epidermis from yolk sac larvae of Pacific herring exposed to ash or sediment for 24 h. A. Control larva. Normal epidermis on the lateral body surface near mid-body. Microridges and cell boundaries are distinct. B. Lateral body surface epidermis from a larva exposed to 1000 mg litre volcanic ash. Note the small puncture- and tear-type abrasions and the particles on the body surface.

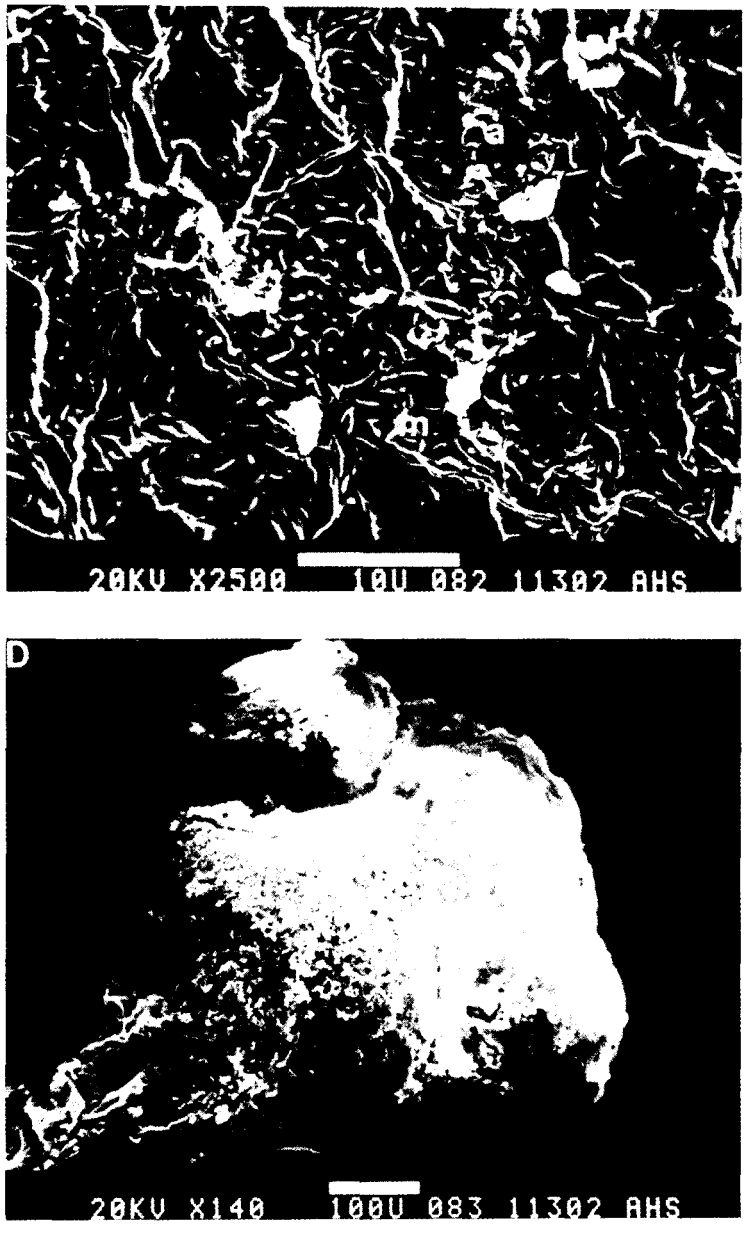

Fig. 2—*contd.*
C. Lateral body surface epidermis from a larva exposed to 8000 mg/litre volcanic ash. The small tears are apparent, as are ash particles. D. Head region of a larva exposed to 8000 mg/litre estuarine sediment. Note the fine layer of sediment coating the head region. a, abrasive damage to the epidermis; m, epidermal microridges; e, eye; s, sediment particles.

of the finfold were normal. Specimens examined from either ash or sediment suspensions, however, showed moderate to abundant particles on the epidermis. Specific abrasion is apparent in the ash experiments, which results in tear- and puncture-type damage rather than a smooth overall abrasion. Puncture wounds at 1000 mg/litre ash were common over the body surface, ranging in size from about 1 to 5 μm (Fig. 2B). The finfold margins were rough compared with the controls. Similar finfold damage was seen on most larvae in ash suspensions. In larvae from 8000 mg/litre ash, puncture wounds and ash particles were apparent on the lateral epidermis, with possibly embedded ash particles (Fig. 2C). In the higher ash concentrations, the ash particles in many cases comprised a fine coating, particularly on the head region. Groups of particles seemed to be maintained in some kind of coating, possibly mucous. The origin of this material is uncertain, however, as mucous-secreting goblet cells are relatively rare in larval herring epidermis.

In the specimens from estuarine sediment experiments, the puncture-type epidermal damage was not as apparent as in the ash experiments. The epidermis generally appeared similar to that of controls with the exception of less distinct microridges and increasing abundance of particles of sediment on the larvae in the higher concentrations. Again, agglutinated groups of sediment particles were most commonly found on the head region (Fig. 2D). Finfold margins were not roughened, as in the ash trials.

DISCUSSION

Egg, as well as larval, stages of fishes are characterized by heightened sensitivity to stress, pollution and physical factors, as compared with later life history stages (Rosenthal & Alderdice, 1976). Within the egg, developing embryos are subject to a wide variety of stresses including elevated temperature, salinity, heavy metals, ultraviolet radiation, lowered dissolved gases and other factors. The embryonic stages, moreover, may be more sensitive at selected critical periods of development (Vladimirov, 1975), when cytological or genetic damage may occur.

When larvae hatch, they no longer have the protection of the chorion. Hunter (1972) and Weihs (1979) demonstrated that newly hatched northern anchovy *Engraulis mordax* larvae depend upon the epidermis for gaseous exchange, a situation typical of many fish larvae. If larvae

develop a coating of particulates over the epidermis, smothering may become a problem for respiratory gas exchange. The epidermis in early larvae, furthermore, is only a few cells thick (O'Connell, 1981; Jones *et al.*, 1966), making larvae subject to abrasion damage and other potentially sublethal effects. Rosenthal (1971) noted that exposure of yolk sac herring larvae to red mud particles resulted in ingestion and potential inability to initiate later feeding. I noted a similar phenomenon of ingestion (Fig. 1C), but later larvae were clearly able to feed (Boehlert & Morgan, in preparation).

Epidermal damage noted on larvae in the suspensions was probably the result of abrasion. Qualitatively, the larval epidermis, as observed at the finfold, was markedly damaged (Fig. 1A). This damage was observed histologically as well (Fig. 1, D through F). While histological damage has been noted in juveniles and adults, no published work shows detrimental effects of sediment or volcanic ash upon histological features of larval fishes. Herbert & Merkens (1961) observed increased healing time for wounds in fish exposed to sediment loads, resulting in higher probability of bacterial infection. Sherk *et al.* (1975) noted a change in the gill structure of white perch exposed to sediments; especially obvious was the increase in the abundance of mucous-producing goblet cells, which presumably aid in removal and sloughing of sediment from the gills. Larvae, however, may lack the ability to remove particles with mucous (Everhart & Duchrow, 1970); indeed, goblet cells are not obvious features of larval herring epidermis and were not abundant under any conditions in the present study. Unpublished findings on the histological changes in yearling chinook salmon exposed *in situ* to volcanic ash suggest marked effects. The epidermis was badly abraded, with approximately one-eighth its normal thickness and loss of all epidermal mucous cells. Pathological conditions were also noted on the gills and pseudobranch, both of which are exposed directly to the ash (T. Yasutake, pers. comm.). This suggests that the sharp glass and crystalline structure of the volcanic ash (Fruchter *et al.*, 1980) may result in cellular and tissue damage greatly beyond that caused by sediment alone.

The results of more recent studies on the histological effects of ash exposure, however, are equivocal. Stober *et al.* (1982) and Redding & Schreck (1982) found no damage to the gill tissue of juvenile salmonids dosed with volcanic ash in the laboratory, despite relatively high dosages. This also points out the differences between effects in the field and laboratory, since Stober *et al.* (1982) also noted significantly higher lethal

levels of ash in the laboratory as compared with the live box bioassays in the field shortly after the eruption. The concentrations of suspended ash and sediment were environmentally realistic for some river locations. Dinehart & Culbertson (1982) observed peak concentrations of 99 000 to 400 000 μg/litre in the Toutle River. Values in the lower estuary, while unknown, are doubtless much lower but may vary as activities such as dredging take place. Thus the possibility of epidermal damage does exist in the field.

In summary, histological work on the yolk sac larvae of Pacific herring showed that both dorsal and ventral epidermal tissues were in significantly poorer condition than controls, apparently from abrasion associated with exposure to volcanic ash. Estuarine sediments caused less extensive damage, affecting the dorsal area only. These effects were apparent as frayed finfolds (Fig. 1B) and the poor condition of the epidermis in higher concentrations of sediment and ash. The abrasive damage noted in these specimens under the light microscope (Fig. 1, E and F) correlated with the damage apparent under the scanning electron microscope, where the presence of puncture-type damage to the epidermis of larvae exposed to volcanic ash was apparent (Fig. 2). Since all of the larvae were alive at the time of preservation, the damage noted probably represents a sublethal effect which would probably have resulted in later mortality.

ACKNOWLEDGEMENTS

The work upon which this publication is based was supported in part by funds provided by the Office of Water Research and Technology (Grant No. 14-34-0001-1461), US Department of the Interior, Washington, DC, through the Washington Water Research Center and the Water Resources Research Institute, Oregon State University. I thank Al Soeldner of the Oregon State University Electron Microscope Facility for assistance and use of facilities and anonymous reviewers for helpful comments on the manuscript.

REFERENCES

Baker, E. & Curl, Jr., H. (1981). Observations of the Columbia River plume after the eruption of Mt. St. Helens. *Coastal Ocean Pollut. Assessment News*, **1**, 1–2.

Boehlert, G. W. & Morgan, J. B. (in preparation). Turbidity enhances feeding in larval Pacific herring, *Clupea harengus pallasi*.

Dinehart, R. L. & Culbertson, J. K. (1982). Sediment-discharge characteristics of the Toutle River following the Mt. St. Helens eruption. In: *Proceedings from the Conference, Mt. St. Helens: Effects on Water Resources*. Water Research Center, Washington State University, Pullman, 99164–302, p. 149.

Dobbs, G. H., III. (1974). Soft tissues of marine teleosts. In: *Principles and techniques of scanning electron microscopy*. (Hayat, M. (Ed)), Van Nostrand Reinhold Co., New York, pp. 72–82.

Everhart, W. K. & Duchrow, R. M. (1970). *Effects of suspended sediment on aquatic environments*. US Bur. Reclam. Proj. Compl. Rep. No. 14-06-D-6596. Colorado State University, 106 pp.

Fruchter, J. S., Robertson, D. E., Evans, J. C., Olsen, K. B., Lepel, E. A., Laul, J. C., Abel, K. H., Sanders, R. W., Jackson, P. D., Wogman, N. W., Perkins, R. W., Van Tuyl, H. H., Beauchamp, R. H., Shade, J. W., Daniel, J. L., Erikson, R. L., Sehmel, G. A., Less, R. N., Robinson, A. V., Moss, O. R., Briant, J. K. & Cannon, W. C. (1980). Mount St. Helens ash from the 18 May, 1980 eruptions: Chemical, physical, mineralogical and biological properties. *Science*, **209**, 1116–25.

Gardner, M. B. (1981). Effects of turbidity on feeding rates and selectivity of bluegills. *Trans. Am. Fish. Soc.*, **110**, 446–55.

Herbert, D. W. & Merkens, G. C. (1961). The effect of suspended mineral solids on the survival of trout. *Int. J. Air Water Pollut.*, **5**, 46–55.

Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, **20**, 1–228.

Hunter, J. R. (1972). Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. *Fish. Bull. US*, **70**, 821–38.

Hunter, J. R. (Ed.) (1976). Report of a colloquium on larval fish mortality studies and their relation to fishery research, January 1975. *NOAA Tech. Rep. NMFS Circ.*, **395**.

Jones, M. P., Holliday, F. G. T. & Dunn, A. E. G. (1966). The ultrastructure of the epidermis of larvae of the herring (*Clupea harenqus*) in relation to the rearing salinity. *J. Mar. Biol. Assoc. UK*, **46**, 235–9.

Martin, D. J., Wasserman, L. J., Jones, R. P. & Salo, E. O. (1982). Effects of the eruption of Mt. St. Helens on salmon population and habitat of the Toutle River. In: *Proceedings from the Conference, Mt. St. Helens: Effects on Water Resources*. Water Research Center, Washington State University, Pullman, 99164-302, 235–252.

Misitano, D. A. (1977). Species composition and relative abundance of larval and post-larval fishes in the Columbia River estuary, 1973. *Fish. Bull. US*, **75**, 218–22.

Muncy, R. J., Atchison, G. J., Bulkley, R. V., Menzel, B. W., Perry, L. G. & Summerfelt, R. G. (1979). Effects of suspended solids and sediment on reproduction and early life of warmwater fishes: A review. *US Environ. Prot. Agency, Corvallis, Oregon*, EPA/600/3/79/042, 202 pp.

O'Connell, C. P. (1976). Histological criteria for diagnosing the starving condition in early post-yolk sac larvae of the northern anchovy, *Engraulis mordax* Girard. *J. Exp. Mar. Biol. Ecol.*, **25**, 285–312.

O'Connell, C. P. (1981). Development of organ systems in the northern anchovy, *Engraulis mordax* and other teleosts. *Am. Zool.*, **21**, 429–46.

Redding, J. M. & Schreck, C. B. (1982). Mt. St. Helens ash causes sublethal stress responses in steelhead trout. In: *Proceedings from the Conference, Mt. St. Helens: Effects on Water Resources*. Water Research Center, Washington State University, Pullman, 99164-302, 300–7.

Roberts, R. J., Bell, M. & Young, H. (1973). Studies on the skin of plaice (*Pleuronectes platessa* L.). II. The development of larval plaice skin. *J. Fish Biol.*, **5**, 103–8.

Rosenthal, H. (1971). Wirkung von 'Rotschlamm' auf Embryonen und larven des Herings, *Clupea harengus. Helgol. Wiss. Meeresunters.*, **22**, 366–76.

Rosenthal, H. & Alderdice, D. F. (1976). Sublethal effects of environmental stressors, natural and pollutional, on marine fish eggs and larvae. *J. Fish. Res. Board Can.*, **33**, 2047–65.

Sherk, J. A., O'Connor, J. M. & Neumann, D. A. (1975). Effects of suspended and deposited sediments on estuarine environments. In: *Estuarine research*, Vol. 2 (Cronin, L. E. (Ed.)), Academic Press, New York, pp. 541–58.

Stober, Q. J., Ross, R. D., Melby, C. L., Dinel, P. A., Jagielo, T. H. & Salo, E. O. (1982). Effect of suspended volcanic sediment on coho and chinnok salmon in the Toutle and Cowlitz Rivers. In: *Proceedings from the Conference, Mt. St. Helens: Effects on Water Resources*. Water Research Center, Washington State University, Pullman, 99164-302, 308–46.

Swensen, W. A. & Matson, M. L. (1976). Influence of turbidity on survival, growth, and distribution of larval lake herring (*Coregonus artedii*), *Trans. Am. Fish. Soc.*, **105**, 541–5.

Vladimirov, V. I. (1975). Critical periods in the development of fishes. *J. Ichthyol.*, **15**, 851–68.

Weihs, D. (1979). Respiration and depth control as possible reasons for swimming of northern anchovy, *Engraulis mordax*, yolk sac larvae. *Fish. Bull., US*, **78**, 109–17.